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Dispersal and extinction in fragmented landscapes

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Evolutionary and population dynamics models suggest that the migration rate will affect the probability of survival in fragmented landscapes. Using data for butterfly species in the fragmented British landscape and in immediately adjoining areas of the European continent, this paper shows that species of intermediate mobility have declined most, followed by those of low mobility, whereas high-mobility species are generally surviving well. Compared to the more sedentary species, species of intermediate mobility require relatively large areas where they breed at slightly lower local densities. Intermediate mobility species have probably fared badly through a combination of metapopulation (extinction and colonization) dynamics and the mortality of migrating individuals which fail to find new habitats in fragmented landscapes. Habitat fragmentation is likely to result in the non-random extinction of populations and species characterized by different levels of dispersal, although the details are likely to depend on the taxa, habitats and regions considered.

Keywords: butterfly; conservation; evolution; mass extinctions; metapopulations

1. INTRODUCTION

Models for the evolution of the dispersal rate are based on a very general trade-off between the benefits and costs of staying or moving (e.g. Gadgil 1971; Van Valen 1971; Roff 1975; Hamilton & May 1977; Comins *et al.* 1980; Hastings 1983; Levin *et al.* 1984; McPeck & Holt 1992; Olivieri *et al.* 1995; Holt & McPeck 1996; Doebeli & Ruxton 1997; Johst & Brandl 1997; Leimar & Norberg 1997; Olivieri & Gouyon 1997; Travis & Dytham 1998). Many of the factors affecting these costs and benefits involve consideration of the size, spacing, quality and temporal variability of particular habitats, the very elements of modern landscapes which have been changed by recent human activities. Therefore, we might expect to see strong selection on existing variation among individuals within species and may also see the differential survival of species which are characterized by different rates of dispersal.

Both evolutionary (e.g. Leimar & Norberg 1997; Travis & Dytham 1999) and ecological (e.g. Lande 1988; Hanski & Zhang 1993) models suggest that persistence and the emigration rate are linked. For example, Travis & Dytham (1999) modelled dispersal in a fragmented landscape and typically generated a bimodal distribution of emigration—high or very low. It makes intuitive sense that there may be a dichotomy in the ways to exploit a severely fragmented landscape, either to be a resident within locally favourable environments or to be highly dispersive with an ability to find and exploit small and isolated patches of resources. However, one could equally plausibly argue the opposite, that organisms with intermediate emigration rates might survive better than either extreme. They benefit from high colonization rates which could compensate for mortality during migration (Hanski & Zhang 1993). These opposite predictions derive principally from specific assumptions made about the costs and benefits of migration.

This paper examines whether mobility and decline are linked. I examine the relationship between the mobility

of British butterflies and declines observed across England, Wales, The Netherlands and Flanders, the landscapes of which are generally severely to moderately degraded. Butterflies are ideal for this because (i) they vary enormously in mobility, from species with a mean intergeneration movement of only 10–20 m right up to intercontinental migrants, (ii) British butterfly species have been categorized into three mobility categories (sedentary, intermediate and wide ranging (Pollard & Yates 1993)) and (iii) historical and recent records are sufficiently good that it is possible to document extinction and decline rates.

2. METHODS

(a) *Mobility classes*

Ecological and evolutionary models of dispersal in fragmented landscapes can conveniently distinguish between movements within habitat patches, fractions of individuals emigrating from their natal habitats, the distances these individuals move and the effects of distance or time on the mortality of migrating individuals. However, adult butterflies use flight for locating adult resources, mates and egg-laying sites within their breeding habitats, as well as for migration between habitat patches. Thus, different dispersal traits tend to be correlated, which is an issue that needs to be considered in future models. For example, one of the more sedentary species is *Plebejus argus*, which has low rates of movement within continuous areas of habitat (mean <20 m), low emigration rates (1.4% recorded exchange), low colonization distances (usually <100 m, but up to 1 km with very rare colonization distances over a few kilometres) and detectable genetic differentiation between local populations (Thomas & Harrison 1992; Brookes *et al.* 1997; Lewis *et al.* 1997; C. D. Thomas, O. T. Lewis and R. J. Wilson, unpublished data). In contrast, *Hesperia comma* is a species of intermediate mobility, with high rates of movement within continuous areas of habitat (mean 88 m in one day within a small area where long distances were hard to record; movements of 1 km recorded), moderate emigration rates (29 and 52% estimated in two different systems), moderate colonization distances (frequent up to 3 km,

with rare colonizations up to 10 km) and a lack of local genetic differentiation (Thomas *et al.* 1986; Thomas & Jones 1993; Hill *et al.* 1996; Thomas & Kunin 1999; J. L. B. Mallet, personal communication).

For the purposes of this study, I used Pollard & Yates' (1993) classification of butterfly mobility, which provides three categories of mobility suitable for an initial examination of the relationship between mobility and persistence. Each of the categories is broad. From mark-release-recapture studies of movements in one to many habitat patches, the mean per generation rate of movement for most species in the sedentary category is between 10 m and 100 or 200 m (usually with up to 20% of individuals emigrating from the natal habitat; frequent colonizations up to 1 km, but rarely beyond), species in the intermediate category move a few hundreds of metres to a few kilometres (usually 10–50% emigrating from the natal habitat, with occasional colonizations up to *ca.* 10 km) and mobile species may move several kilometres and often much further (100% emigration at the scale of typical landscape elements; colonization cannot be easily distinguished from individual movement). Of the true migrants, only *Cynthia cardui*, *Vanessa atalanta* and *Colias croceus* were included. These three categories are hereafter referred to as mobility classes.

(b) *Multi-region analysis*

The first analysis examines extinction from 21 regions. Extinction from each region generally represents the loss of many breeding areas. The regions are Bedfordshire (Arnold *et al.* 1997), Berkshire–Buckinghamshire–Oxfordshire (Asher 1994), Cambridgeshire (Bennett & Perrin 1994), Derbyshire (Harrison & Sterling 1985), Devon (Bristow *et al.* 1993), Essex (Corke 1997), Flanders (Maes & Van Dyck 1996), Gwynedd excluding the Llandudno area (Whalley 1997), Hertfordshire (Sawford 1987), Kent (Philp 1993), the Llandudno area (Cowley *et al.* 1999; C. D. Thomas, O. T. Lewis and R. J. Wilson, unpublished data), the London area (Plant 1987), The Netherlands (Tax 1989; Van Swaay & Plate 1996), Norfolk (Hall 1991), Northumberland–Durham (Dunn & Parrack 1986), Shropshire (Riley 1991), Suffolk (Mendel & Piotrowski 1986; Stewart 1996), Surrey (Collins 1995), Sussex (Pratt 1981; Gay & Gay 1996), Wiltshire (Fuller 1995) and Yorkshire (Sutton & Beaumont 1989). A list of historically recorded butterfly species was established for each region. In most cases, the authors of each regional account discussed the veracity of the older records for that area and their advice could be taken. In some cases, information on the historic distributions had to be supplemented from Heath *et al.* (1984) and Emmet & Heath (1990).

In a very few cases, the veracity of recent records was in doubt and again I took the advice of the regional author. The regional accounts were then used to determine whether each species which had originally occurred in a region was still extant. If a species had become extinct historically but had recolonized since, it was regarded as still surviving in that region. If the only recent populations of a species in a given region had arisen from documented introductions, the species was regarded as extinct.

Each species was thus given a score for regional persistence, varying from 0 (extinct from all regions from which it was originally recorded) through to 1 (surviving in every region from which it had been recorded historically). Species which were extinct from every region were then excluded to ensure that at least some suitable habitat and/or climate still existed within the region considered.

(c) *Dorset analysis*

This second analysis is more akin to an assessment of population-level rates of decline. It is based on the English county of Dorset, for which two regional atlases have been published (Thomas & Webb 1984; J. A. Thomas *et al.* 1998)—note that this county was excluded from the multi-region analysis. J. A. Thomas *et al.* (1998) presented a summary table of the number of 1 km grid squares occupied by each species for two time-periods (1970–1984 and 1980–1994), where a 1 km grid square will generally contain one to several breeding areas for each species. These time-periods are the most recent time categories used for plotting distributions in the two atlases. Although the periods overlap partially, it is still reasonable to use them to assess population changes (the patterns would just be stronger if the time-periods were mutually exclusive).

I calculated a value for the distributional change for each species in Dorset. The later time-period contained more records than the earlier period, which gives a false impression of increases in certain species, so I adjusted the estimated rates of change to take some account of this. It is reasonable to assume that the small white butterfly *Pieris rapae* would have been recorded from every grid square in both time-periods, given sufficient sampling effort. I regarded this species as not having changed its distribution at 1 km resolution. Therefore, I expressed the changes in all other species as changes relative to the number of *P. rapae* records. The number of 1 km grid squares in which each species was recorded in 1970–1984 was divided by 1557 and the number recorded for each species in 1980–1994 was divided by 2139 (the respective number of *P. rapae* squares for each period). The value for the more recent period divided by the value for the older period was then used as a measure of change (<1 = decline and >1 = increase). This procedure simply results in a rescaling of the values (it multiplies observed change by a constant) to make them easier to interpret and in no way affects the statistical significance of the relationship between mobility class and change.

(d) *Mobility and minimum area*

Warren (1992; updated from Thomas (1984)) listed the minimum areas within which colonies of particular species could be contained (for the purposes of conservation). No time-limit was placed by Warren (1992) or Thomas (1984) on the expected period of persistence, but the implication was that such colonies could persist for several to tens of generations and sometimes for longer. If they were completely isolated, these colonies would be unlikely to be self-sustaining in the long run: each such area is generally part of a larger population system. Nonetheless, they give an indication of the relative area requirements of a range of species. Here, I examine whether species which differ in mobility have different area requirements. All species listed by Warren (1992) are included, comprising 32 sedentary species and 14 species of intermediate mobility. Mobile species and a few of the most mobile intermediate species were not assigned minimum areas by Warren (1992) and were excluded from the analysis.

(e) *Statistics*

In the multi-region analysis, nearly half (27 out of 56 species) of the species still survived in every region from which they had been recorded, so it was not possible to transform the data to be normally distributed. Differences in the extinction proportions within the three mobility groups were analysed using a Kruskal–Wallis test adjusted for ties. In the Dorset analysis, the values for

change were approximately normally distributed, so change in status between mobility groups was analysed by one-way ANOVA. For minimum areas, the area values designated by Warren (1992) were ordinal categories, so the data were analysed with a Mann–Whitney *U*-test.

Comparative (phylogenetic) analysis of the relationship between mobility and distributional change was not attempted because it was not possible to develop a clear hypothesis to predict how an evolutionary increase (or decrease) in mobility would affect persistence. For example, an evolutionary increase from sedentary to intermediate (one level of mobility increase) might decrease persistence, whereas a further increase in mobility from intermediate to mobile (also one level of mobility increase) might increase persistence; it is not possible to infer from this whether a change from sedentary to mobile (two levels of mobility increase) should result in an increase, decrease or no change in persistence. The rank order of expected persistence is uncertain and not necessarily the same as the rank order of the evolutionary sequence for changes in mobility (relatively sedentary \leftrightarrow intermediate \leftrightarrow mobile). Because of this mismatch, it is not then possible to calculate meaningful average mobility values for any branch of the phylogenetic tree which contains all three dispersal values (as regards testing the hypothesis that intermediate mobility confers highest or lowest survival).

Inspection of the data suggested that the observed results were generated by species from within all but three of the major groups of butterflies. Of these, Papilionidae and Riodinidae were represented by single species and could be included without any problem. However, all species in the subfamily Satyrinae had both a characteristic mobility (sedentary) and high persistence in the multi-region analysis (this subfamily did not have unusually high levels of survival in the Dorset 1 km resolution analysis). Therefore, I reanalysed the results without this subfamily.

3. RESULTS

(a) Multi-region analysis

Out of the 56 species, 29 belonged to the sedentary mobility class, 17 were intermediate and ten were mobile. There was a trend for the regional extinction rate to be highest for species of intermediate mobility (median survival = 0.60), lower for sedentary species (median survival = 0.95) and lowest for mobile species (median survival = 1.0) (figure 1; Kruskal–Wallis $H = 5.50$, d.f. = 2 and $p = 0.064$). There was little effect of reanalysing without the seven species of Satyrinae ($p = 0.072$).

(b) Dorset analysis

Out of the 46 species, 23 were sedentary, 14 intermediate and nine mobile. Regional declines were steepest for species of intermediate mobility (mean change \pm s.e. = 0.828 ± 0.088) and lower for sedentary species (mean change \pm s.e. = 0.911 ± 0.048), while records of mobile species tended to increase (mean change \pm s.e. = 1.132 ± 0.069) (figure 2; ANOVA $F_{2,43} = 3.807$ and $p = 0.030$). The result was similar after omitting the Satyrinae ($p = 0.028$).

(c) Mobility and minimum area

On average, the 32 sedentary species do not require such large areas of habitat (mean *ca.* 2 ha) to sustain colonies, as

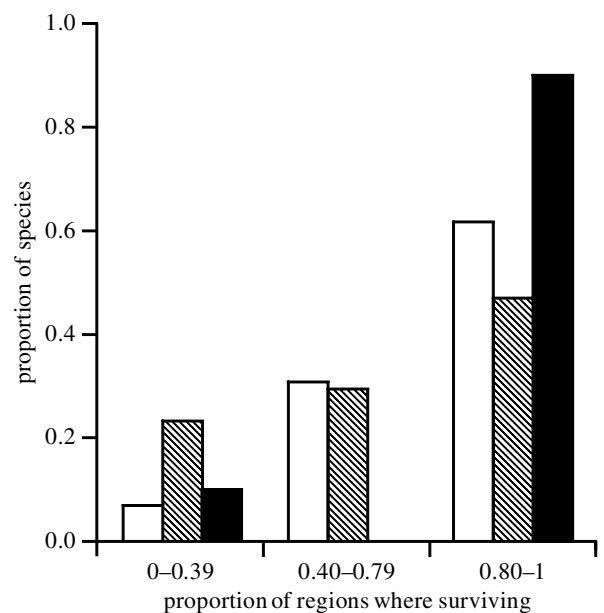


Figure 1. Proportions of 21 regions where butterfly species still survive as a function of butterfly mobility: open bars, sedentary species; hatched bars, intermediate species; black bars, mobile species.

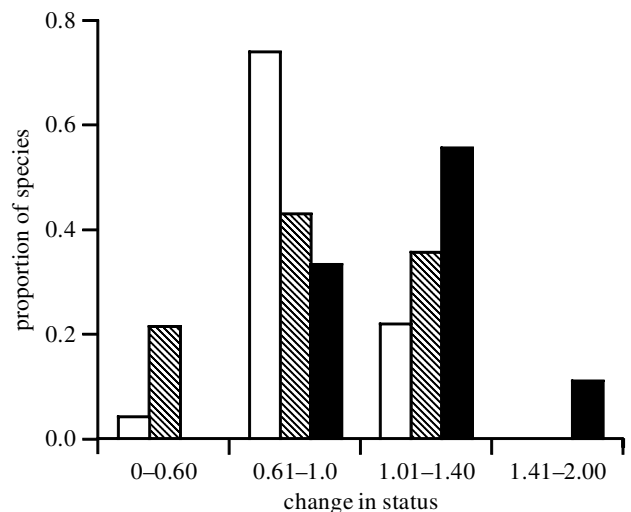


Figure 2. Rate of population change in the UK county of Dorset, between 1970–1984 and 1980–1994, as a function of butterfly mobility: open bars, sedentary species; hatched bars, intermediate species; black bars, mobile species. Data from Thomas & Webb (1984) and J. A. Thomas *et al.* (1998).

do the 14 species of intermediate mobility (mean *ca.* 12 ha) (figure 3; Mann–Whitney *U*-test $N_1 = 32$, $N_2 = 14$, $W = 634.5$ and $p = 0.0032$).

4. DISCUSSION

Testing the hypothesis that extinction rates will be different for species with different levels of mobility is difficult because one would expect huge changes in status to be observed within each mobility class, depending on the differences in the extent to which the habitats of different species have declined (or increased in some cases). Butterflies in all mobility classes will decline if

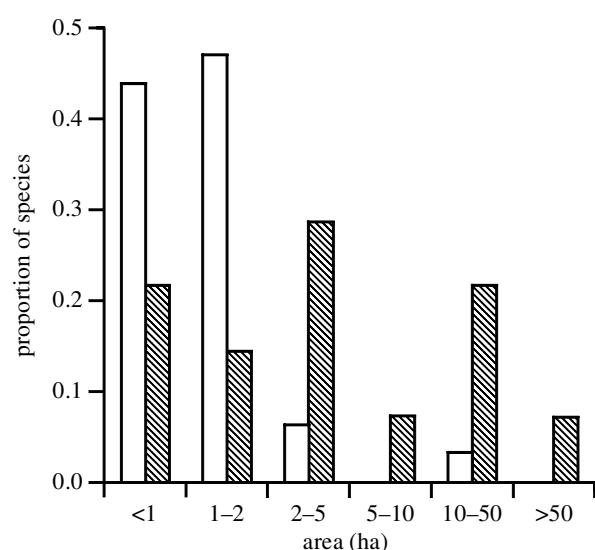


Figure 3. Minimum habitat area requirements (from Warren 1992) for species which are relatively sedentary (open bars) and of intermediate mobility (hatched bars).

their habitats decline. Likewise, if a particular type of habitat has been relatively unaffected by modern landscape changes, species using those habitats should survive relatively well, regardless of their mobility. Figures 1 and 2 show that some species of intermediate mobility are indeed surviving well. Despite the expected noise in the data arising from different species inhabiting different habitats, there was a general trend for species of intermediate mobility to survive less well than both sedentary and mobile species in the landscapes considered.

Species of intermediate mobility could be associated with particular characteristic habitat types which have shown the steepest declines in the study region or they might be associated with habitats which are particularly unstable naturally (with high rates of local extinction due to succession and/or disturbance) (Thomas & Morris 1995). Such factors are certainly important, but do not appear to be responsible for the pattern reported here. Ranking each species crudely as occupying either stable (e.g. woodland, scrub and intermediate-tall grassland) or unstable conditions (e.g. fresh disturbances, heavily grazed grasslands and fresh woodland clearings), there were no significant differences between the three mobility classes in the proportions of species occupying stable versus unstable habitats (regional analysis $X^2=1.38$, d.f. = 2 and $p \approx 0.5$ and Dorset analysis $X^2=0.40$, d.f. = 2 and $p > 0.5$). Considering specific habitats, butterflies associated with freshly created woodland clearings are known to have declined particularly steeply, in line with the decline in coppicing (traditional cutting of woodland on a short rotation) (Heath *et al.* 1984; Emmet & Heath 1990; also mentioned in most of the regional atlases). However, this affects more sedentary (four) than intermediate-mobility (two) species.

The observed pattern of the steepest declines among species of intermediate mobility is the opposite of that predicted by the ecological model of Hanski & Zhang (1993), but accords with the general conceptual conclusions of some evolutionary models (e.g. Travis & Dytham

1999). We should not interpret the match between the empirical results and the evolutionary models too literally because the models concentrate on emigration fractions, whereas the Pollard & Yates (1993) mobility classes incorporate blends of knowledge of rates of movement within habitats, proportions of individuals emigrating from their habitats and the distances achieved by these individuals.

We require population dynamics explanations for the observed patterns because the evolutionary models do not relate to between-species patterns of change. First, consider isolated patches of habitat and only consider species of low and intermediate mobility. Local selection will favour reduced rates of emigration, as emigrants leave and fail to be replaced by immigrants (e.g. Den Boer 1990; Dempster 1991; Olivieri *et al.* 1995; Cody & Overton 1996; C. D. Thomas *et al.* 1998a). However, a reduced emigration rate may not evolve fast enough to save populations from extinction. For a given habitat area, intermediate-mobility species will suffer a higher per capita drain of individuals than more sedentary species. This may render them more susceptible to stochastic extinction and, in the extreme, drive them deterministically extinct if the number of individuals lost to emigration each generation exceeds the number that can be replaced by the reproductive output of those that stay (e.g. Game 1980; Buechner 1987; Stamps *et al.* 1987; Thomas & Hanski 1997). A quantitative analysis of two species of butterfly showed that the more mobile species required a predictably larger minimum area in which to survive (Thomas & Hanski 1997; C. D. Thomas *et al.* 1998b). The analysis of minimum colony areas across a wider range of species is consistent with this hypothesis: species of intermediate mobility require larger habitat patch areas than do sedentary species, with an approximately sixfold difference in minimum area requirements (figure 3). The approximately two- to four- (plus)fold increase in linear dispersal distances from sedentary to intermediate-mobility species (see §2) would lead one to expect intermediate-mobility species to require four to 16 (plus) times the areas in which to survive (given the same level of recognition of habitat boundaries, the same level of environmental stochasticity and no immigration). Similarly, Woodroffe & Ginsberg (1998) showed that carnivores with large home ranges require larger national parks to survive, because species with large home ranges suffer increased per capita mortality outside the parks. Therefore, not only does individual selection favour reduced emigration from small, isolated populations, but population dynamics result in the extinction of populations in which the levels of mortality due to emigration are too high.

In most metapopulation models, the local extinction probability is linked to the local population size, a phenomenon which is strongly supported by empirical evidence (Hanski & Gilpin 1997; Hanski 1999). Treating mobility as a continuous variable, Cowley *et al.* (2000) showed that mobility and population density, where present, are correlated using both standard regression and phylogenetically controlled independent contrasts ($p < 0.01$ in both analyses). On average, species of intermediate mobility (mean density = 5.50 butterflies per transect per season) have 34% lower local population sizes than sedentary species (mean density = 8.32 butterflies per

transect per season) for a given patch area. Therefore, one would expect species of intermediate mobility to have an approximately 1.5-fold larger area requirements than sedentary species. It is not yet possible to identify whether increased emigration of species of intermediate mobility is responsible for the difference in the observed density or whether other factors are partially or wholly responsible (e.g. resource densities or natural enemies). Increased mobility may be a cause of low densities in fragmented landscapes or it may represent an ecological or evolutionary response to low density (e.g. the need to find mates and resources and avoid inbreeding).

At the level of individual habitat patches, there is some support for both hypotheses: increased emigration and small local population size (and the interaction between them) may render species of intermediate mobility more susceptible to local extinction than sedentary species. The same arguments can be extended to entire networks of habitat patches. For a given landscape, metapopulation theory (Hanski & Gilpin 1997) predicts that networks of smaller populations (intermediate mobility) could survive less well than networks of larger populations (sedentary species), provided that the increased extinction rate in intermediate species is greater than the reduced colonization by sedentary species. Emigration from natal habitats can also potentially threaten entire population systems. In studies of metapopulations of two butterfly species, *ca.* 15–35% of all individuals have been estimated to die between patches (Hanski *et al.* 1999; Thomas & Kunin 1999). This drain of individuals may be sufficient to increase the system-wide (stochastic) probability of extinction and may explain the absence of the same species from more severely degraded landscapes, where mortality due to migration would be even higher (i.e. in systems where patches are smaller and more isolated). This has already been observed in theoretical models (Lande 1988; Hanski & Zhang 1993). A population system will not persist if the total mortality due to migration is higher than can be sustained by the reproductive output of individuals within breeding habitats.

These complementary arguments imply that species become extinct long before the last fragment of suitable breeding habitat is lost, both because of metapopulation dynamics and because of mortality due to emigrating individuals which fail to arrive successfully in other patches. Once habitat is heavily fragmented, the burdens of emigrant mortality and extinction from very small patches are higher for intermediate-mobility than for sedentary species and so they are likely to disappear first. Suitable breeding habitats should still survive in many regions, but there are inadequate quantities of habitat for populations to be dynamically viable. This is borne out by the history of butterfly introductions and reintroductions in Britain, which are often successful for a few years, but only very rarely succeed over periods of decades (Oates & Warren 1990). It is also confirmed by the widespread occurrence of empty, but apparently suitable breeding habitats for butterflies in many fragmented landscapes (Thomas & Harrison 1992; Thomas *et al.* 1992; Thomas & Jones 1993; Thomas & Hanski 1997; Hanski 1999).

Both sedentary and intermediate-mobility butterflies tend to breed in identifiable habitats, which become

fragmented in modern landscapes. If mobile species behaved in the same way, the previous arguments could be used to suggest that highly mobile species should survive even less well than do species of intermediate mobility. In fact, mobile species readily move across heterogeneous landscapes, they are generally large and long lived as adults and they may delay adult reproduction until some time after emergence (Thomas 1984; Warren 1992; Hodgson 1993; Pollard & Yates 1993). Before recent landscape changes took place, they were already well designed to seek out and use small and often ephemeral patches of resources scattered across the landscape. Modern landscapes represent altered distributions of adult and larval resources, but the butterflies are merely exploiting their pre-existing reproductive and flight strategies. In that respect, recently fragmented landscapes do not present new challenges.

Not all taxa will show the same pattern. Longer lived and even more intelligent organisms may exhibit greater abilities to avoid leaving isolated patches of habitat and may be better at relocating them if they do. For example, taxa which possess distinct dispersal polymorphisms, occupy a completely different range of body sizes (e.g. thrips and birds), walk rather than fly and show much narrower ranges of variation in their dispersal rates may not show the bimodal pattern of survival shown here. Some of these organisms may show unimodal relationships between migration and persistence and the direction of the relationship may differ between groups. If the quantitative patterns of costs and benefits of migration differ, some taxa may even show greatest survival of species of intermediate mobility.

The levels of fragmentation, speed of fragmentation and natural dynamics of the original vegetation will have crucial effects on the relationship between migration rates and the probability of persistence. Most of the landscapes considered in this study are already moderately to severely degraded. For example, one of the least degraded landscapes considered is around Llandudno in North Wales, where 77% of the landscape is extremely poor for butterflies (urban, improved fields, non-habitats and sports fields), and where individual butterfly species cover only 1.44% (median) of the land surface (Cowley *et al.* 1999). The observed pattern relating mobility and extinction might be completely different in initially intact landscapes suffering from the first stages of habitat modification or in even more highly degraded landscapes at the end of the process. When fragmentation is so severe that almost all habitat fragments are very small, local extinction rates may be high for all species. Sedentary species would then be the worst affected, because they would have the lowest rate of recolonization following inevitable local extinctions, as suggested for Flanders by Maes & Van Dyck (1999).

Despite the likelihood that the observed patterns will depend on both the taxa and landscapes considered, the general phenomenon of a link between rates of movement and persistence in fragmented landscapes is likely to be widespread. Humans have had major impacts on terrestrial landscapes and appear to be initiating a major extinction event (May *et al.* 1995). It is reasonable to assume that some of the organisms which disappear will be characterized by traits which are unsuited to survival

during the current period of environmental disruption. Certain traits, such as being a wide-ranging carnivore (Woodroffe & Ginsberg 1998), being a predator-naïve inhabitant of an oceanic island (Pimm *et al.* 1995), having particular habitat associations (Thomas & Morris 1995) or simply having a small geographical range (Gaston 1994) may render species particularly susceptible to extinction. The migration rate is one trait which would be expected to have a particularly strong effect on survival probability in recently fragmented, terrestrial landscapes. The results presented here provide some evidence that this effect is already manifesting itself.

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